

# MESOSPERM PALYNOLOGIC EVIDENCE AND ANCESTORS OF ANGIOSPERMS

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## ABSTRACT

Late Triassic and mid-Cretaceous appear to have been times of evolutionary innovations of seed plant pollen. Between these times dispersed pollen indicates relatively little change, although megafossil studies record the appearance of several new plant groups in the late Jurassic. This incongruity suggests that knowledge of pollination arrangements of Mesozoic seed plants is far from complete; some plants have been described with stigmatic surfaces, and investigation of their morphological intermediate position needs much fuller attention. The search for Mesozoic ancestors of angiosperms is particularly difficult because of the lack of a satisfactory definition of an angiosperm in Cretaceous time. It is suggested that all Mesozoic seed plants should be placed in a Mesosperm Group of fossils and that no living angiosperm taxon should be used for fossil plant remains before the Cenozoic unless at least two separately preserved plant organs in the same beds can be shown to be associated in supporting that taxon. All Mesozoic seed plant taxa should be based solely on evidence from fossils.

In this short paper my object is to attempt to clear some of the obscuring fog around the problem of angiosperm ancestors. Hitherto, on the basis of the current understanding of the terms 'gymnosperm' and 'angiosperm,' I have supported (Hughes, 1976) the view that certain Cretaceous Barremian pollen represented the earliest angiosperms and that any ancestor should properly be sought among gymnosperms in earlier Cretaceous rocks. Progress, however, has been relatively slow because only a small proportion of those interested in the problem work with newly discovered fossil evidence. At the Ninth Botanical Congress (Montreal 1959), the struggle for understanding against obscure diversion (cf. Scott et al., 1960; Hughes, 1961) centered on supposed cryptogenic upland plants; more recently diversions take the form of lightly documented curiosities of comparative morphology of pollen aperture and exine structure (e.g., Klaus, 1979; Cornet, 1980).

In this age of advanced techniques of study of the available abundance of microfossils, a solution to the whole problem actually seems to be attainable by painstaking production of good records of fossils alone. The dangers to such continuous progress by hard work appear to lie in poor communications resulting from ill-defined terms and in the impatience commonly expressed through unnecessary neobotanical association theories. After examining briefly the current progress with fossil gymnosperms, I shall turn to definitions of terms and to those classi-

fication procedures that appear to obstruct understanding.

## LATE TRIASSIC POLLEN INNOVATIONS

Schulz (1967) described pollen of *Clavatipollenites* type from the late Triassic of Poland. Klaus (1979) amplified the description of the tri-saccate *Dacrycarpites europaeus* Mädlar (1964) to include various angiosperm aperture and exine characters that he compared with the pollen of *Schizandra* and other living plants; but these 'prae-angiospermid' characters were observed on 'occasional aberrant' grains. Cornet (1980) referred to a wide range of late Triassic angiospermid apertures but the information is provided only in unillustrated abstract form and is thus difficult to use. If the material referred to by these authors were subjected to rigorous recording with adequate specimen numbers and statistical assistance, it seems likely that some new information would emerge.

In addition, late Triassic is the time of origin of *Classopollis*, *Eucommiidites*, and *Ovalipollis*, all of undisputed gymnospermid character; Scott (1960) compared *Equisetosporites* with *Ephedra*. In comparison, therefore, with the periods of geologic time just before and just after, these late Triassic floras appeared to have been involved in unusual innovations of pollen characters (Text-fig. 1).

This period of time also produced the megafossil *Sanmiguelia* claimed by Cornet (pers.

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Stratigraphic Scale	'Atlantic-area' Megafloras	Seed Plant Events				
		Pollen	Flower	Fruit	Leaf	Wood
Cenomanian			F5			W2
Albian	Potomac 35° Cr N	P3				
Aptian					L2	W1?
110						
Barremian	Wealden 40° Cr N	P2		Fr1		
Hauterivian						
Valanginian						
Berriasian						
135+						
	Morrison 40° Jr N		F4			
Late Jurassic						
Mid Jurassic	Yorkshire 40° Jr N		F3			
Early Jurassic						
195+	Scania 40° Jr N East Greenland 45° Tr N		F2			
Rhaetian					L1	
Norian			P1			
Carnian			F1			

TEXT-FIGURE 1. Stratigraphic table of seed plant occurrences and of Atlantic-area floras with approximate paleolatitudes. P1 = Late Triassic pollen innovations; P2 = tectate columellate monocolpate pollen; P3 = tricolpate pollen. F1 = *Sturiantus*; F2 = *Williamsonia*; F3 = *Williamsoniella*; F4 = *Cycadeoidea*; F5 = angiospermid inflorescences. Fr1 = *Onoana*. L1 = *Sanmiguelia*; L2 = Potomac leaves. W1 = *Aptiana* Stopes; W2 = undisputed vessel-bearing wood.

comm.) to be of angiosperm nature. Just such a claim was also made by the original author (Brown, 1956) but had subsequently been doubted because of the state of preservation (Doyle, 1973). The new better preserved material could change opinions.

#### CRETACEOUS BARREMIAN POLLEN INNOVATIONS

Tectate columellate monosulcate pollen has now been recorded (Hughes et al., 1979) from the British Wealden strata in a succession of many palynologic samples from Berriasian age onwards in which the entry and diversification of such pollen within Barremian time is firmly documented. Unfortunately, there are no useful megafossil plants from the Barremian strata concerned.

Pollen of this type has been recorded by Doyle and Robbins (1977) and others from the Potomac Group of eastern North America where there are well known megafossils redescribed by Hick-

ey and Doyle (1977). The stratigraphic information about these non-marine beds is not complete, but some of the earliest megafossils probably came from approximately Barremian-Aptian boundary times (Potomac—Zone I); there is however an unconformity below and thus no downward succession into earlier beds. Doyle (1982) records a valuable advance in knowledge down-dip, but much more information is still needed.

With the arrival of 'angiospermid pollen' there is a sudden incoming and diversification of large numbers of '*Ephedripites*' pollen. This is also an innovation, but the other palynomorphs in the assemblages are not new and include normal Cretaceous representative species of *Classopollis* (see Alvin, 1982) and *Eucommiidites*.

Although the equivalent beds in West Africa (Doyle et al., 1977) have produced an extended number of types of 'angiospermid' pollen, the stratigraphic succession does not show for certain that the critical palynomorph zones C-V and C-VI are of Barremian rather than of early Ap-

tian age. There are, however, zones C-IV and below, which comprise a downward succession and lack this pollen.

The striking fact about all these Cretaceous successions is that these major Barremian pollen innovations are the first since Rhaetian times. Palynomorphs from many described Hettangian to Hauterivian samples may bear spore innovations such as *Cicatricosisporites* in the late Jurassic and *Aequitriradites* in the early Cretaceous but there are virtually no new or unusual pollen types representing the seed plants.

#### JURASSIC PLANT MEGAFOSSILS

The relative lack of new variety in seed plant pollen in the Jurassic is contrasted with what is known of the major plant groups themselves. The Bennettiales diversify in the Jurassic into Williamoniaceae, Wielandiellaceae and, towards the end of the period, Cycadeoidaceae. The Nilssoniales are apparently distinct and diverse throughout; despite attempts using single plant organs as far back as the Permian to identify them with living Cycadales, the situation remains confused and it seems more helpful to confine any discussion of true Cycads to the Cenozoic (cf. Krassilov, 1978: 896). The large group of 'Ginkgophytes,' including *Karckenia* and *Pseudotorellia*, became important in late Jurassic and early Cretaceous time; it is in many ways unfortunate and misleading that the group should even bear the name of the one living species of *Ginkgo*. There is continuous diversification of what are broadly known as Jurassic Coniferales. Entirely new groups such as the Pentoxylales also arose in this time interval.

Despite strong suspicions that some of these plant fossils such as *Caytonia* and *Leptostrobus* (Czekanowskiales) included early kinds of stigmatic surface, there still appears to be no significant appropriate pollen modification. Insect contacts with plant reproductive systems may well have been confined at first to the Coleoptera but in latest Jurassic and early Cretaceous time both the Diptera and the Hymenoptera appear to have evolved far enough to be concerned, but again this is without any apparent response in the pollen morphology before Barremian time.

This striking incongruity of evidence between pollen and megafossils may have some other explanation, but it is probably due to our lack of appreciation of the scope and diversity of the Mesozoic gymnosperms. One of the main causes

of this lack is the continued fitting of all fossil plant evidence of this age into a neobotanical hierarchical classification that is inappropriate and irrelevant but is almost always used by custom; the continuation of this procedure perhaps represents the biggest outstanding failure of paleobotany.

Also, as can be seen in Text-figure 1, the main floras, on which most of the interpretations are based, were located in a narrow belt of northern mid-paleolatitudes. Megafossil occurrences in both southern and high northern paleolatitudes are well documented, but the palynologic evidence is more fragmentary as yet.

#### DEFINITIONS OF MAJOR GROUPS

The term 'angiosperm' is easily and acceptably defined in the world of present-day plants on the basis of a combination of the fossilizable characters of the flower, fruit, pollen, leaf, and wood. However, in mid-Cretaceous time there is normally available, at any one locality, only one plant organ such as pollen or fruit or leaf with its one set of characters. For example, it is by no means certain that the unseen Albian plants providing tectate columellate tricolpate pollen also possessed reticulate-veined laminate leaves; in fact what is known of the order of appearance of organs and characters suggests incongruity of development. Thus it is questionable whether the Barremian tectate monocolpate pollen mentioned above should be included in Angiospermae; but if it is not so included, then no other comparable single organ occurrence can be included either and the question of evolution from ancestors becomes unanswerable. Although an arbitrary decision to include such Barremian pollen in Angiospermae can be made, the case will remain unsatisfactory because the whole of the rest of the Barremian plant concerned could well prove to have gymnospermous characters; no appropriate flower, fruit, leaf, or wood has yet been found at this stratigraphic level.

Correspondingly, the term 'gymnosperm,' in the Mesozoic, is dependent on antithesis and is negative in that it includes any seed plant not shown to be an angiosperm. Further, the term 'flowering plant' must now include Bennettiales and several other pre-Cretaceous gymnospermous fossils and so cannot be used in place of angiosperm.

Thus, if the major terms cannot be defined for Cretaceous time it is meaningless to nominate

## MESOZOIC SEED PLANTS

Recommended classification	Terms for Cenozoic use only
<b>MESOSPERM GROUP</b>	Gymnospermae
Brachyphylls	
Cheirolepidiaceae	
Linearphylls	Coniferales
'Ginkgoaceae' (temporary use)	Ginkgoales
Czekanowskiales	
Bennettitales	
Nilsoniales	Cycadales
Caytoniales	
Irania group	
Dirhopalostachys group	
Pentoxylales	
Cretasperm group	Dicotyledones (Magnoliopsida)
Cretablum group	
Cretapoll group	
Cretaphyll group	
Cretoxyl group	
	Monocotyledones (Liliopsida)
	Magnoliales
<b>ANGIOSPERMAE</b>	
(Only for those pre-Cenozoic records in which two separate organ fossils have been accepted as associated thus confirming the presence of a formally recognized angiosperm taxon.)	

TEXT-FIGURE 2. Scheme of classification of Mesozoic seed plants. List of groups is representative only, but includes some formal groups with latinized name endings. The five Cretaceous single-organ groups are informal. The names in the right-hand column are excluded in this scheme from Mesozoic use.

any Cretaceous, Jurassic, or Triassic fossil as the earliest angiosperm, and such exclusion must apply also to the Barremian pollen.

#### PROPOSAL FOR MESOZOIC CLASSIFICATION OF SEED PLANTS

The failure of definitions just mentioned can be overcome simply by classifying fossils by those features alone that are observed, omitting all reference to features that are merely supposed. In the present case, there appears to be no dispute that the fossils concerned represent seed plants and that their general sequence age is also known. Hence, it would be logical to attribute all such Mesozoic seed plants to a new 'Mesosperm Group,' which is a name for a group defined to receive all fossil orders or families of Triassic, Jurassic, or Cretaceous age displaying any undisputed seed plant characters; the name 'Mesosperm Group' is neither latinized nor typified so that it remains outside the current neobotanical hierarchy. Thus, the formal name Gymnospermae would not be defined or required in the Mesozoic and would be restricted merely to Recent and Cenozoic plants; any Paleozoic use could be similarly avoided with ease. For the Mesozoic,

the use of such subordinate subjective units as Coniferales, Cycadales, Ginkgoales, and Araucariaceae at the family level could also with advantage be avoided for the same reason. As indicated on Text-figure 2, all currently used fossil seed plant groups would be included in the Mesosperm Group.

#### ANGIOSPERM TERMINOLOGY TRANSITION FROM MESOZOIC TO CENOZOIC

Even from the late Cretaceous most angiospermous plant evidence is still in the form of individual records of separated flower, fruit, pollen, or leaf; for any records in this state it is appropriate that they should stay in the Mesosperm Group. The criterion, therefore, for change to formal inclusion in Angiospermae could well be the accepted proof of association of two separated organs, e.g., the flowers with Normapolles type pollen referred to by Friis (1981, 1984) and by Skarby (1981). Such a criterion could even provide stimulus to exploration and would greatly enhance the value of fully worked records. Cenozoic angiosperm records would for convenience be free of this restriction.

#### REFERENCE TO CRETACEOUS ANGIOSPERMID CHARACTERS

From Barremian and Aptian times onwards to the end of the Cretaceous, numerous pollen or leaf or other fossils have already been attributed to extant angiosperm families; although the attributions are harmless expressions of opinion in themselves, the use for the record of a name directly reflecting the indication of affinity is undesirable because it depends, in virtually every case, on the characters of only one organ.

Clearly, such weakly based records should not be accorded the same status as the important cases of accepted confirmation mentioned in the previous section. The undoubted cumulative value of such unconfirmed records can best be expressed by neutral group terms such as 'Cretasperm' and 'Cretaphyll' for communication and listing purposes (see Text-fig. 2); in construction of these words the use of general age and general morphology indications seem unlikely to mislead, but the lack of a latinized ending emphasizes the distinct origin and purpose of such names. The extension of that system of names to include 'Triassopoll' or 'Juraphyll' as required, appears reasonable. Undoubtedly, some authors concerned with 'Cretaphylls' and 'Cretapolls' may consider their single organ evidence to be very strong but the requirement to prove association appears to be an appropriate restraint that will recall for all users the true state of the record.

In this connection, the very well-documented compilation of Muller (1981) appears to present a few cases for exemption from this structure, because he limited his Cretaceous 'acceptances' so severely. Muller (1981: 6) himself drew attention to the problem of lack of information about other organs than pollen, and the logical need for confirmation that remains. It is probably better that work should be stimulated on acceptable confirmation of even these few Cretaceous pollen claims to family or higher group identification, by treating them in the same way as all other single organ records.

#### ADVANTAGES OF PROPOSED MESOSPERM GROUP SCHEME

1) The scheme outlined above and illustrated in Text-figure 2 involves minimum disturbance to current practice and literature, and calls for additional activity only in classifying Cretaceous 'angiosperms.'

2) The status of records is automatically and much more clearly indicated.

3) Although not directly suggesting a polyphyletic origin for angiospermy, the scheme leaves the matter truly open by removing all trace of classificatory bias towards a monophyletic theory that has no base in geological history nearer to the Cretaceous than 60 million years.

4) The idea, developed for many years in his writings by the late Professor Tom Harris, that paleobotanists are only on the edge of understanding the true biologic range of Mesozoic seed plants, will be strengthened.

#### CONCLUSIONS

1) Clearly some more-botanically-based colleagues will tend to be dismissive of this scheme, but I ask them to look beyond the apparent iconoclasm. The purpose is to tackle the problem of which the solution has eluded both botanists and geologists for a very long time, by attempting to reorganize the available data, separately from all theory, so that entirely new studies may be encouraged.

2) No solution to the main problem is offered here. Such a solution will appear only gradually when all available evidence has been encompassed. I am personally convinced that there is no abnormal tangible factor involved beyond ordinary paleontological experience.

3) Although perhaps entirely unbiased data handling is unattainable, it appears worthwhile in this way to attempt to free a virtually deadlocked topic.

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